

What is a population?

- ♦ Defining population/geographic limits essential to fishery studies
 - Species = individuals of two or more populations capable of interbreeding and producing viable, fertile offspring
 - E.g., Great Lakes/Pacific coast salmon
 - Population = group of a species that interbreeds = gene flow
 - Dynamic unit: share common mortality, growth, recruitment patterns = basic unit of fishery population dynamics models
 - May/may not be geographically defined (e.g., salmon/tuna populations range widely over ocean and congregate only during spawning season)

Many factors influence population structure and dynamics

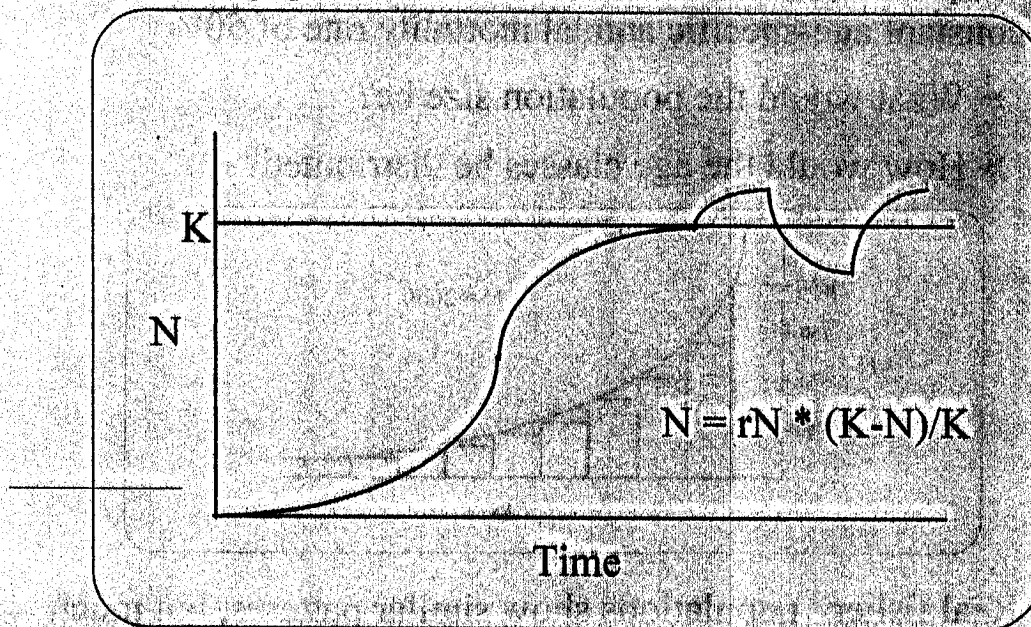
- ♦ Inherent biological traits affect population abundance, potential yield, and fishing strategy
 - Age at 1st spawning re: generation time
 - Longevity re: number of adult age classes/individual size
 - Age-specific fecundity and natural mortality rates usually decline with age, so relative number of juveniles in population influenced by ages of adults
- ♦ Environmental conditions affect survival (e.g., abiotic events, predation and growth (e.g., temperature, food supply))
 - Heavy fishing pressure depletes large/leaves small fish
 - Absolute size of a population (e.g., overcrowding may deplete juveniles due to competition w/ superior adults; LO alewives)
- ♦ Relative age class numbers and distributions can tell a fishery biologist much about conditions influencing a population

Population size limited by capacity to increase and carrying capacity of environment

- ♦ Conceptual model is $CI_{(t1-t0)} = [P_{t0} * RP * SP * ER] = P_{t1} - P_{t0}$
 - CI = capacity for increase, t = time, P_t = population size at time t, RP = reproductive potential, SP = survival potential, ER = environmental resistance
 - Based on classical Lotka-Volterra equation

$$l = \int_0^x e^{-rx} * l_x * m_x,$$
 where r = intrinsic rate of natural increase,
 l_x = probability of survival to age x
 m_x = number of offspring per female in year x
 - RP = inherent genetic factors that determine the number of offspring produced by a female (value > 1)
 - Related to 'r' and m_x functions of logistic equation
 - SP = ability of an organism to survive the exigencies of life
 - Influenced by genetics, acclimation history, niche
 - Related to l_x and m_x functions of equation (value < 1)
 - ER = environmental factors reduce RP additions to and lower SP of population
 - Related to l_x function (value < 1)
 - For typical fish populations, RP is high and SP is low (especially for eggs/larvae/juveniles)
 - High populations result only in "good" years when ER low
 - When RP and SP are both low, populations always

- The classical Carrying Capacity (K) model is often used by fishery scientists to model the potential for fish population growth and ultimate population size



- Model characterized by rapid (exponential) population growth when population small, followed by cyclic overshoots/declines as environmental conditions fluctuate naturally

Oscillations may dampen = stable environmental conditions
or they may increase = unstable conditions

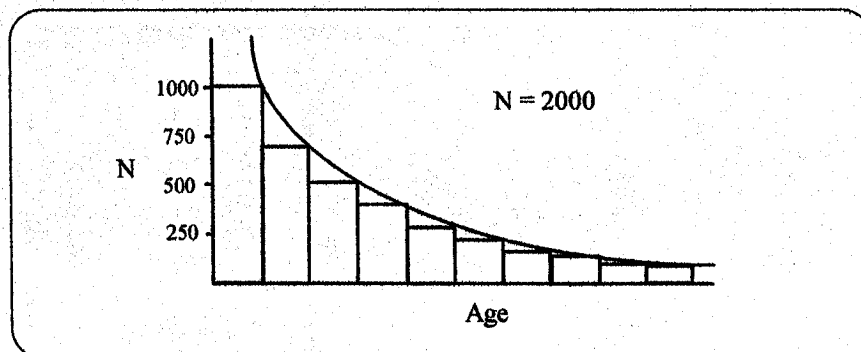
- In the real world, 'K' is a moving target

Space, food supplies, physical/chemical conditions, competitors, predators, weather, etc. establish a variable, average 'K' for each habitat and population

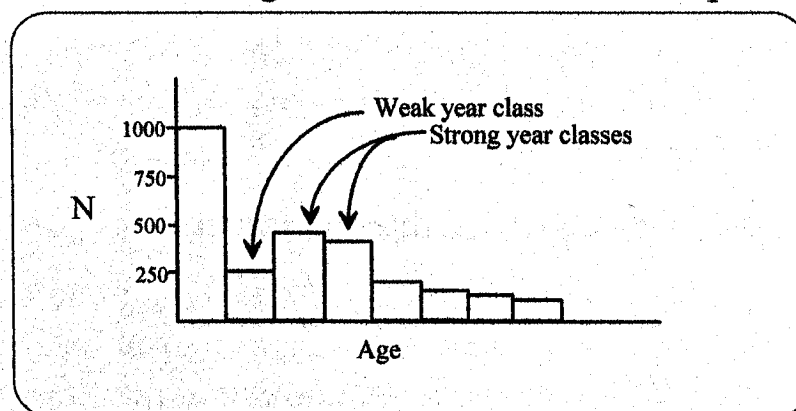
- Humans are major predators of fish who seek to keep fish populations perpetually in their exponential growth phase to provide large numbers of healthy fish for a fishery

Theory/reality of population size/age class distributions in a fishery

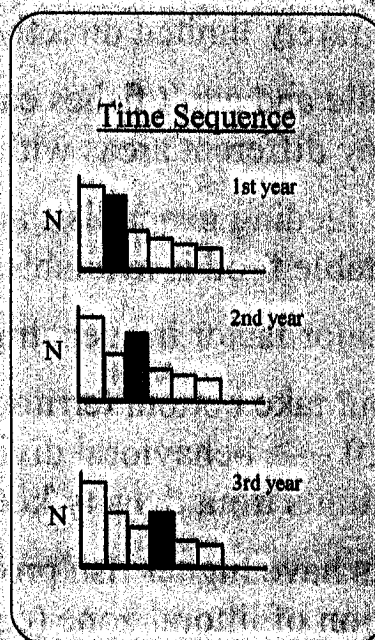
- ♦ Suppose a population adds 1000 recruits per year and has a constant age-specific annual mortality rate of 50%
 - What would the population size be?
 - How would the age classes be distributed?



- ♦ Real fishery populations show similar patterns, but much variation occurs due to greatly differing year class strengths
 - What factors might cause these relationships?



- Strong/weak year classes visible in age class diagrams for years (e.g., 1978 classes of alewives/yellow perch in LO)



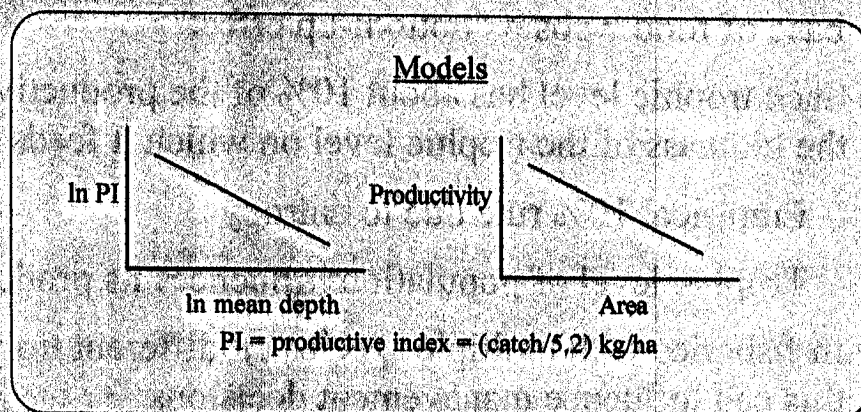
Populations fluctuate in response to many environmental factors

- ♦ Essential plant nutrients, particularly nitrate and phosphate, determine the fertility of water for phytoplankton/other plants at the base of food webs = "bottom-up effect"
 - Each trophic level has about 10% of the productivity/25% of the biomass of the trophic level on which it feeds
 - Empirical 10% rule due to entropy
 - Trophic level of population influences its production/yield
 - In fisheries with multiple species on different trophic levels this can influence management decisions
 - Food production: manage for species low in food web
 - Sport/fish size: manage higher in food web (e.g., herring vs. swordfish)
- Different age classes usually occupy different trophic levels
 - E.g., larvae eat plankton; juveniles eat invertebrates and small fishes; adults eat larger fishes or invertebrates

- Population size rarely limited directly by food supplies
 - Larval, juvenile and adult fishes eat different foods and usually occupy different areas within the population range
 - Most fish are feeding generalists and will switch to/eat whatever suitable food is available
- ♦ Physical space a major factor influencing K in fish populations
 - E.g., stream trout take bottom territory based on volume of invertebrate drift ---> behavioral division of environmental resources that limits trout density/keeps fish healthy
 - Smaller habitats have higher fish production/unit area due to greater proportion of littoral zone (e.g., 200+ lb fish/acre in 1 acre pond; vs. 1.5 lb/acre in 5 million acre lake)

Similar for nearshore vs. offshore marine/Great Lakes

- Solid relationships between productivity and lake area/depth



- Relationship holds for GL ranked by depth/production

<u>Rank Scale</u>	<u>Mean depth</u>	<u>% < 100 ft</u>	<u>Production</u>
small	Erie	Superior	Superior
	Huron	Michigan	Ontario
medium	Michigan	Ontario	Huron
	Ontario	Huron	Michigan
large	Superior	Erie	Erie

- ♦ Interspecific competition: fish can compete over almost any resource, especially spawning sites, shelter, access to food
 - Rarely direct competition for food due to broad feeding habits, common prey switching, and ability to stunt growth

E.g., alewives in LO do all of these; populations stay large

- To demonstrate competition for food, 3 things must be known

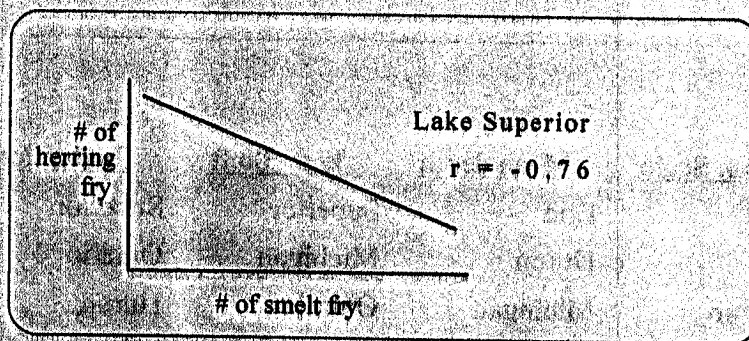
Food supply is limited

All available food is being used

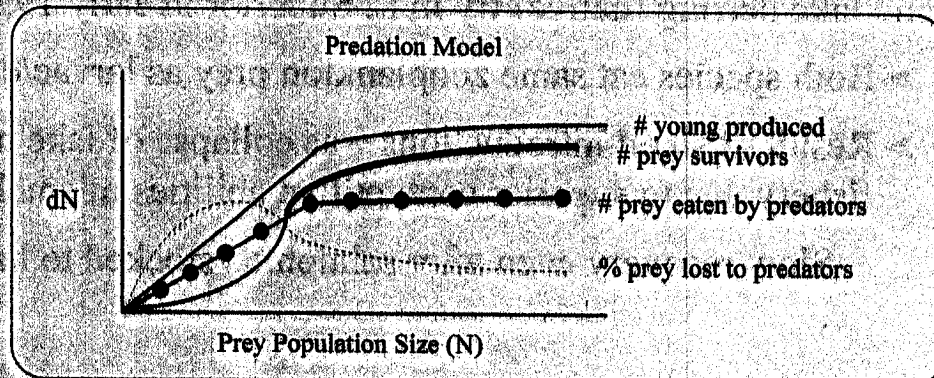
The two species in 'competition' have the same food habits and do not shift to alternate food sources

Requires extensive field sampling/fish gut contents analysis

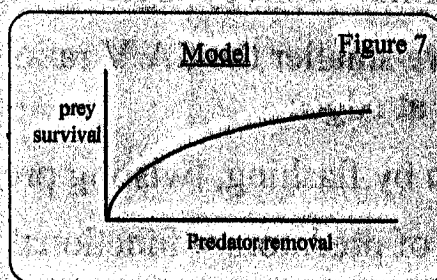
- ♦ Direct example: food competition between rainbow smelt (exotic) and lake herring (native) fry in L. Superior in early 1970s
 - Both species eat same zooplankton prey as larvae/don't switch
 - Result of smelt introductions was collapse of lake herring fishery due to superior competitive abilities of smelt
 - Slow recovery even after salmonids stocked to harvest smelt



- ♦ Predator-prey relationships strongly influence fish populations
 - Predator and prey populations can interact three ways
 - Numerical response: as prey population goes up or down, predator populations follow in lagged cyclic pattern
 - Functional response: individual predators eat more prey from abundant prey species
 - Developmental response: relative maturity/experience of individual predators influences their feeding efficiency
 - Magnitude of predator influence on prey is related to the relative abundance of predator and prey species
 - Predator populations usually limited by spawning site availability, territory size, etc., so potential numerical response to increasing prey populations limited
 - Fixed predator population impact on prey population directly related to prey population size



- ♦ Sometimes, fishery biologists can dramatically improve prey population abundance by predator control/harvest



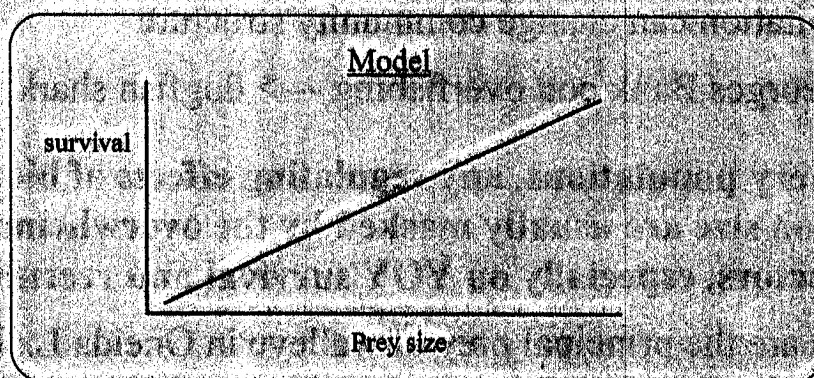
- Opposite problem may be to add predators to control out of control prey populations

E.g., salmonids in GL to control alewives

- Size of individual prey may influence predation and prey survival rates
- Small fish, especially young of the year (YOY), particularly vulnerable to predation; can escape by growing to large size quickly

E.g., inverse relationship for sockeye salmon between the number of outmigrating smolts and their average size

Predation intensity so heavy on numerous, smaller fish that fewer, larger fish provided higher adult returns to fishery

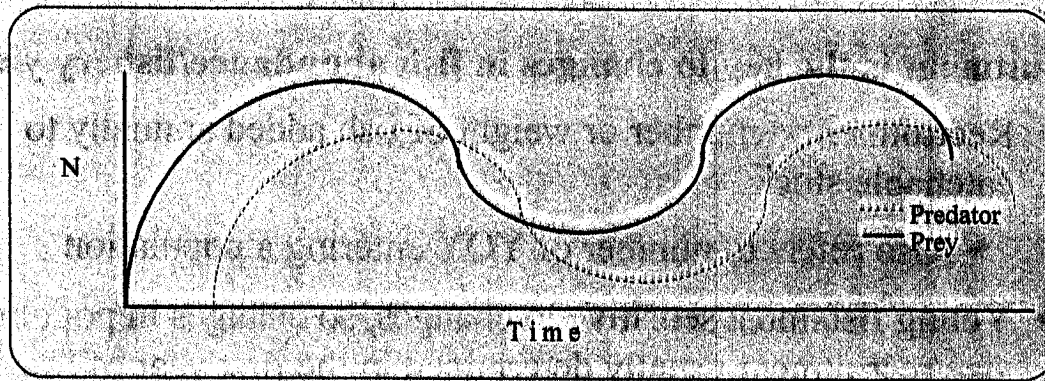


Growth rates of fish may critically influence survival rates

- Prey behavior influences predator effectiveness (schooling)
 - Prey are harder to find = convoy logic
 - Bigger schools have smaller the SA/V ratio = fewer fish exposed to attacks at edges
 - Predator confusion by flashing, twisting prey
 - Eventual satiation of predators = functional response
- ♦ Example of fishery population changes due to competition and predation acting together: Great Lakes
 - Sea lamprey predation/overfishing eliminated burbot/lake trout
 - Alewife introduction into predator vacuum ---> competition with native planktivores/predation on their eggs/larvae
 - Alewives replaced most native whitefishes, chubs, herrings and created a much simplified, unstable ecosystem
 - To compensate, fishery managers introduced exotic salmonids and use chemical controls for lampreys
 - When alewives crashed in L. Michigan in 1983, native bloaters returned
 - Is restoration of original ecosystem possible?
- ♦ Exploitation can change community structure
 - Georges Bank cod overfishing ---> dogfish shark fishery

In most fishery populations, any regulating effects of biotic factors on population size are usually masked by the overwhelming effects of abiotic factors, especially on YOY survival and recruitment

- ♦ Perch are the principal prey of walleye in Oneida L., but their populations usually fluctuate together vs. shifted cyclic phases expected of pure predator-prey relationships; Why?



- Abiotic variables (temperature, wind) affect both populations in the same way/time

Wash floating perch egg strings onto beaches and crush walleye eggs in shallow water gravels

Classic example of abiotic factors overshadowing biotic relations in determining fish population abundance

Recruitment is the key to changes in fish abundance/fishery yields

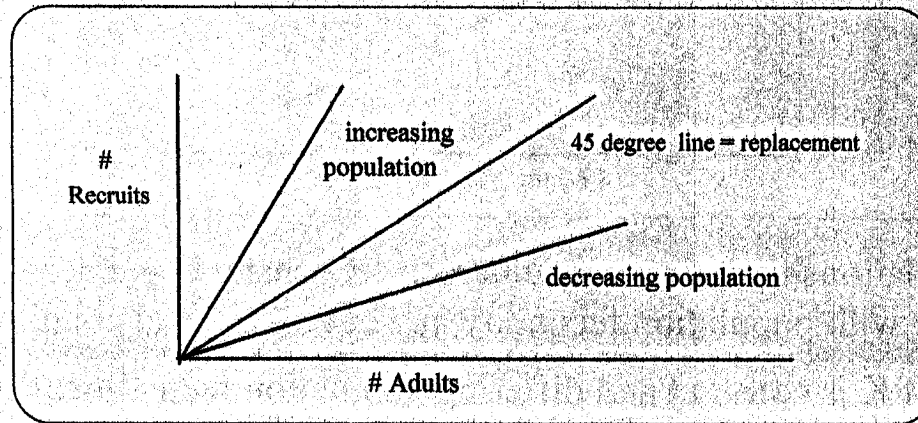
- ♦ Recruitment = number or weight of fish added annually to catchable stock
 - Also refers to number of YOY entering a population
- ♦ Young fish most sensitive to changes, so changes in population size/recruitment usually determined in the first year of life

What factors influence recruitment?

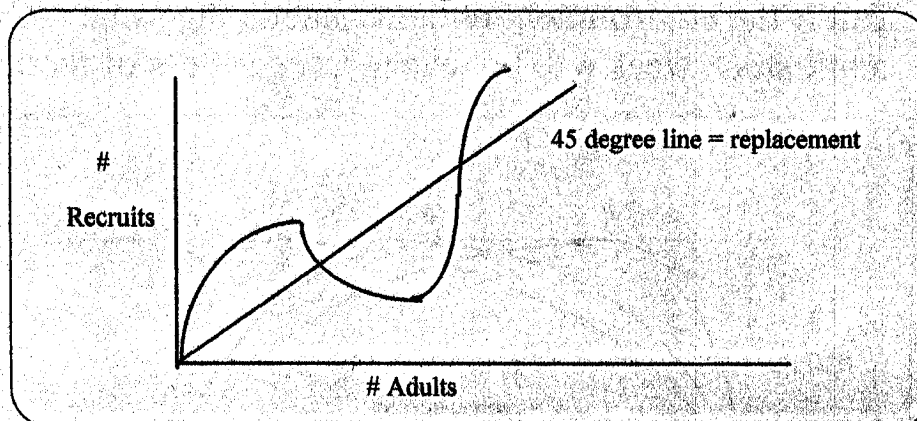
- ♦ In theory, changes in parent stock size should affect recruitment
 - Larger adult stock should leave fewer resources for recruits = compensatory or density dependent relationship and vice versa
 - E.g., Nest site competition forces some spawners out of optimum habitats (poor YOY survival)
 - Destruction of earlier redds by later spawners (salmonids)
 - Increased starvation of/cannibalism on YOY
- ♦ Depensatory effects = inverse density dependent relationship
 - With a constant number of predators or a constant environmental stress, as the # of YOY decreases, the % mortality increases
 - E.g., as YOY # decreases, predators work harder to maintain constant food intake which depletes YOY more rapidly than when #s are high
- ♦ Extrapensatory effects = density independent relationship
 - Death of YOY due to extrinsic factors like temperature, drought, floods, pollution, etc.
 - Effect is independent of adult/YOY population sizes
 - This mortality is the major influence on YOY strength, but recruitment models based on density-dependent relationship

Density dependent models of adult/recruit relationship

- ♦ In theory, recruits should just replace adults long term (otherwise, populations will trend up or down)

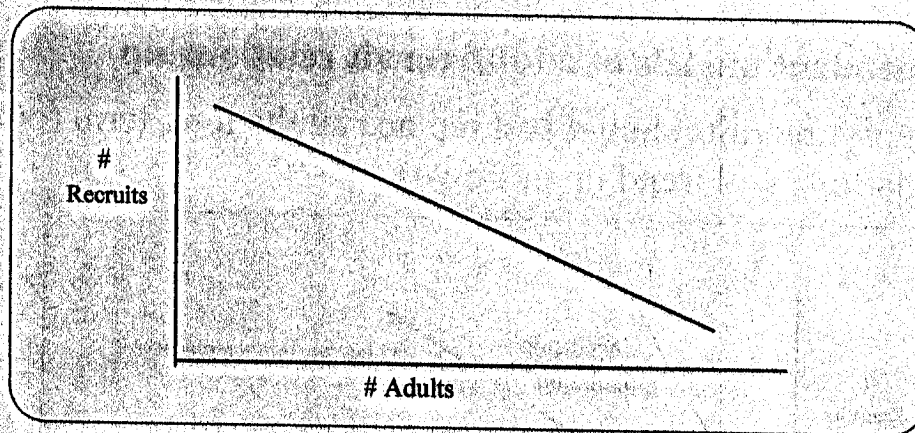


- ♦ In reality, the relative numbers of recruits and adults fluctuates widely due to density independent effects on YOY numbers



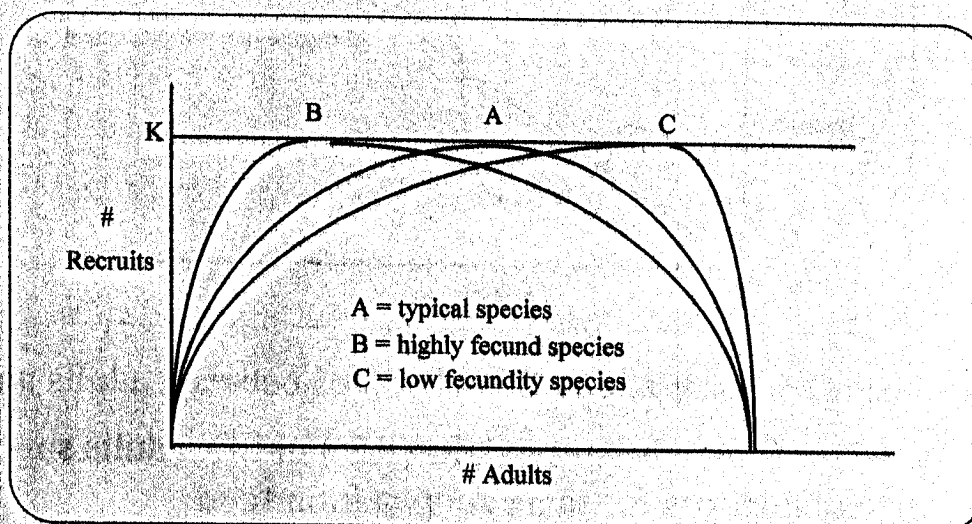
- ♦ Negative correlation often observed between adults and juveniles
 - Age II alewives vs. adults (III+) in LO: adults superior competitors for same zooplankton food
 - Similar situation for Age I and YOY rainbow smelt in L. Ontario has produced alternating strong year classes

Strong Age I cohort feeds heavily on YOY that produces a small Age I cohort the next year that permits a large YOY cohort to survive ----> 2 year abundance cycles of smelt



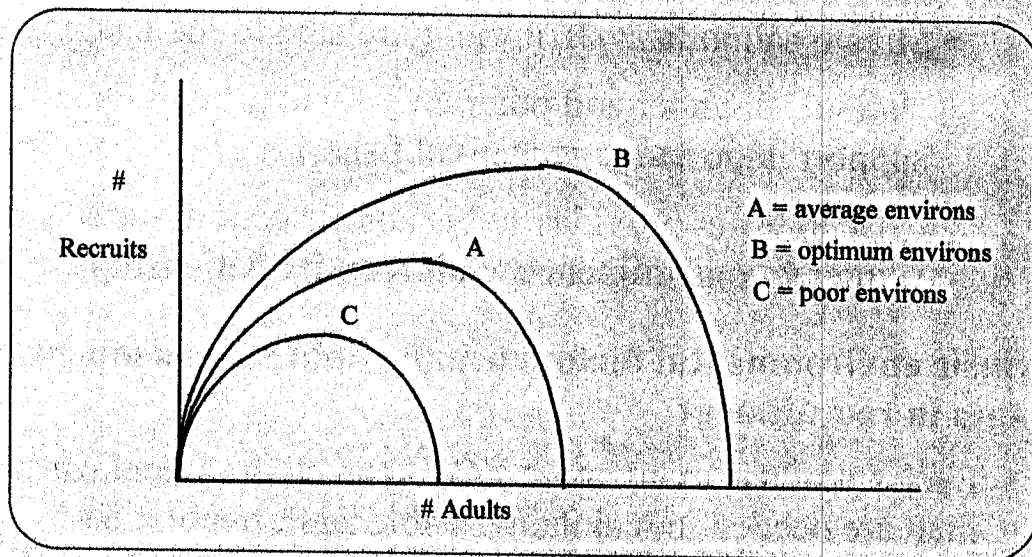
- ♦ If relationship between adults/recruits density dependent, it will vary with population fecundity and environmental conditions
 - If K is constant and differing population fecundities are assumed, then a highly fecund species will fill the environment sooner than average and low fecundity species

But if the environment remains stable, the same recruit and adult stock sizes will be reached, regardless of fecundity



- If fecundity is constant and K (environ conditions) changes, more adults and recruits will be present in better environments

But regardless of fecundity, a good environment ----> more YOY surviving to recruitment ----> larger adult stock



- ♦ These curves are hyperbolas following the general equation $Y = aS - bS^2$, where $S = \# \text{ adults}$ and $Y = \# \text{ recruits}$
 - Called a reproductive curve, this function has important properties that conform to real world conditions/make it useful
 - Larger populations occur in better environments
 - A given # adult produces more recruits in better conditions
 - When $S = 0$, $YOY/\text{recruits} = 0$
 - Conditions can be so severe that no matter how large S is, $YOY/\text{recruits} = 0$
 - Can develop a model by sampling $YOY/\text{recruits}$ and S for many years
 - Does a relationship exist?
 - If so, in the future you can predict recruitment by sampling only the adult population size or vice versa
 - The latter ability would be very nice to predict harvest quotas for the future in a fishery
- ♦ Examples of populations in which there is a density-dependent relationship between adults and recruits

- Stream salmonids: territoriality related to food supply
- Halibut, flounder and other long-lived ground fishes that support important commercial fisheries

Deep water provides stable abiotic conditions so biotic interactions influence adult/recruit relationship

Extrinsic environmental factors usually obliterate compensatory changes in recruitment

- ◆ Fishes produce many more YOY than environment can support or than are needed to maintain a stable adult population

- Subsequent losses in response to abiotic (mainly) and biotic environmental conditions adjust recruitment to fit fluctuating environmental carrying capacity (K)

E.g., walleyes lay eggs loosely on bottom cobbles/cracks exposed to many environmental influences

Heavy rain/freezing temperatures destroy year classes

Lowest walleye spawning rate in years ----> largest YOY class ever in Red Lakes, MN: perfect conditions

- Short-lived, small commercial fishes (herrings, sardines, etc.) have such enormous fecundity that environmental conditions always determine recruitment

E.g., for North Sea herring, YOY survival is related to food availability when larvae hatch, not adult stock size

- L. Erie blue pike illustrates complex relationships

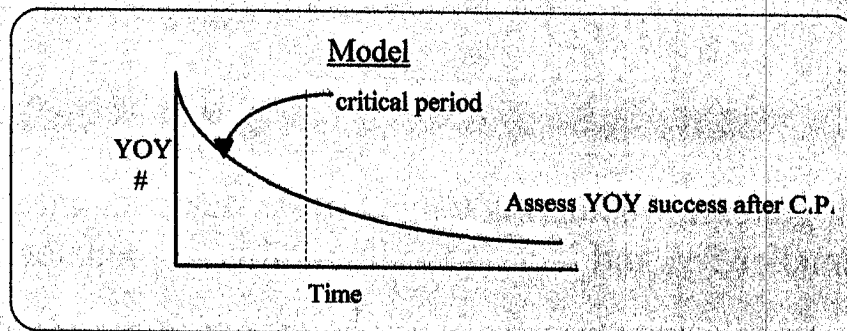
Thought to be nearly extirpated in the 1960s, then over a million pounsa harvested in one year

Probably due to perfect environ conditions for YOY survival several years earlier

Final overharvest did in the fishery; none caught in 20 years

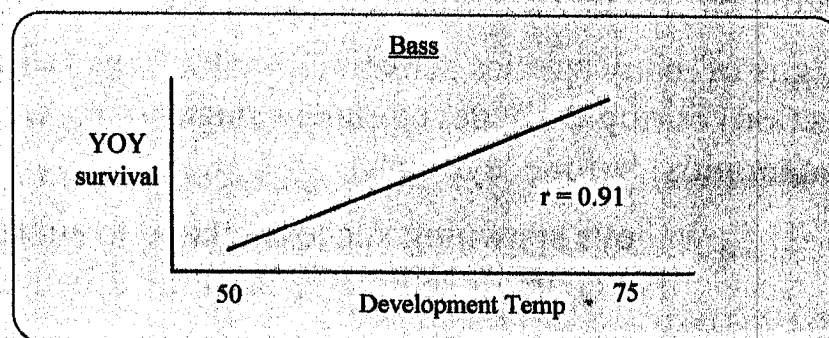
Why is the larval-juvenile stage so important?

- ♦ Critical period is the very rapid decline in YOY numbers that occurs from fertilization to first independent feeding
 - Time with highest mortality is from yolk-sac resorption (maternal nutrition) until live food captured
- YOY extremely vulnerable to starvation/increased predation as they expose themselves in active searches for food



Many extrinsic factors influence year class strength

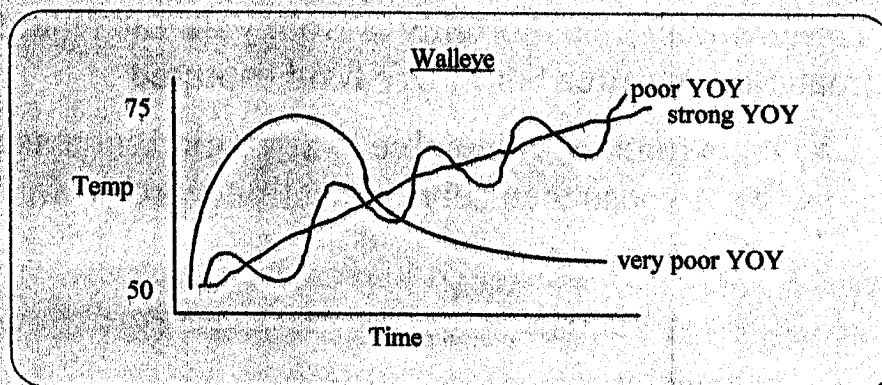
- ♦ Correct timing of environmental conditions and hatching is critical to successful recruitment
- ♦ Temperature influences metabolic rates by Q_{10} effect in ectothermic fish which influences growth rates and progression through developmental stages
 - For largemouth bass, the critical period between hatching and leaving the nest (2-4 weeks post-hatch)



➤ Walleye YOY strength depends on spring temperature regimes

Adults move into streams to spawn when temps > 50 F

Water temperature immediately after spawning most critical



➤ In general, fluctuating temperatures delay hatching, produce smaller fry, and increase vulnerability to predators, floods, etc.

In extreme cases there can be lack of temporal association between food availability and YOY feeding requirements

♦ Wind affects YOY and their food supplies, especially pelagically spawned fish or fish hatched in wave zones

- Can sweep pelagic eggs onto beaches (e.g., yellow perch egg strings in Oneida L.)
- Can transport eggs and larvae away from nursery areas (e.g., Georges Bank haddock)
- Eggs and larvae buried/ground by winds/currents moving sediments (e.g., bass spawn in shallows)
- Eggs of many species sensitive to vibrations (wind/wave action) during early development stages (e.g., walleye, salmonids) before "eye-up"

E.g., walleye spawning success related to substrate: highest survival in coarsest sediments least disturbed by winds

➤ Wind also influences food availability ---> nutrient upwelling

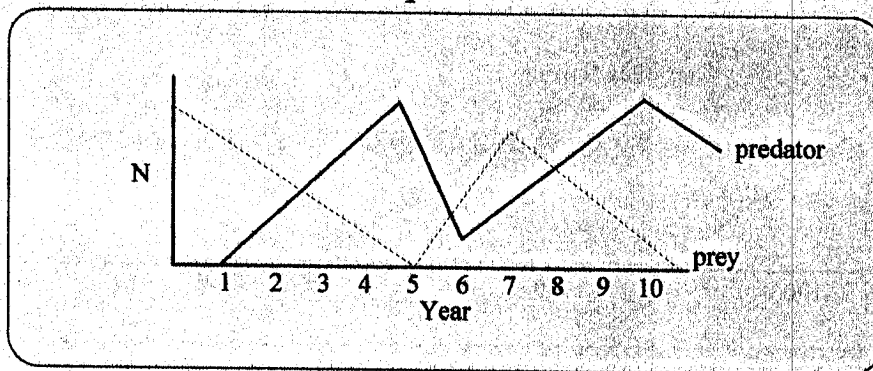
- ♦ Water level and rainfall influence YOY survival/recruitment
 - E.g., positive correlation between June rainfall and rockbass/walleye YOY strength probably due to water level over spawning beds and nutrient increases from runoff
 - Rain storms have opposite effect due to scouring, turbidity, currents
 - Rainfall/stream levels important for anadromous stream fishes
 - Salmon ascend coastal streams after first fall rains
 - Odor cues provide guidance and higher water permits passage upstream (e.g., Trask River)
 - Movements of radio tagged fish in and out of L. Ontario tributaries vs. rain/flows (Keleher et al. 1985)
 - Whitefish and lake trout spawn on shoals in GL
 - If water too low, winter ice scours redds or crushes eggs
 - If water too high, fry can't rise to surface to fill gas bladder
 - Undesirable species can be eliminated or thinned by manipulating water levels during their spawning season
 - Drown or expose redds/YOY (e.g., panfish, carp)
- ♦ Chemical composition of water may influence YOY survival
 - Changes in ocean or freshwater chemistry that affect fishery population dynamics are rare except for pollution events
 - YOY life stage most sensitive to these changes
 - Estuarine fisheries sensitive to salinity
 - E.g., Hurricane Agnes in 1973 flooded Chesapeake Bay w/ freshwater and shifted oyster distributions down the bay
 - Prolonged drought shifts saltwater species farther up the bay

- Unusual local edaphic conditions can influence recruitment
 - E.g., Fe and Ca leaching from iron and limestone rich areas
 - E.g., Se leaching from CA irrigation practices affect fish/waterfowl
- ♦ Food availability strongly affects recruitment
 - Generally predators and prey fluctuate together relative to abiotic changes in the environment, so a balance is maintained
 - Winds may sweep plankton or YOY out of feeding area or change upwelling patterns to reduce/increase water fertility
 - E.g., El Nino effect = southern oscillation: atmospheric temperature changes change ocean currents and temperatures and impact S. American anchovetta fishery, bird nesting, etc.
- ♦ Catastrophies are extrapensatory effects that can dramatically affect YOY and recruitment, as well as adult populations
 - E.g., winter ice cover/summer thermal stratification both cause oxygen depletion and fish kills in nutrient enriched waters
 - E.g., red tides, floods, drought (dried up Mississippi R. in 1988), etc.

How is population size affected by recruitment processes?

- ♦ Annual/"random" fluctuations in recruitment are intrinsic to all fisheries
 - In a well managed fishery, fluctuations oscillate about a stable mean
 - Fluctuations are damped or accentuated by abiotic or biotic changes in the environment

- Most fish mortality takes place in the egg and YOY stages, so year class strength and ultimate adult population size is set early in life history
- ♦ Cycles are periodic fluctuations in year class abundance
 - Oceanic climate cycles are fairly common
 - 50 year herring cycle off Norway observed for 700 years
 - Related to ocean temperature related to solar activity cycle



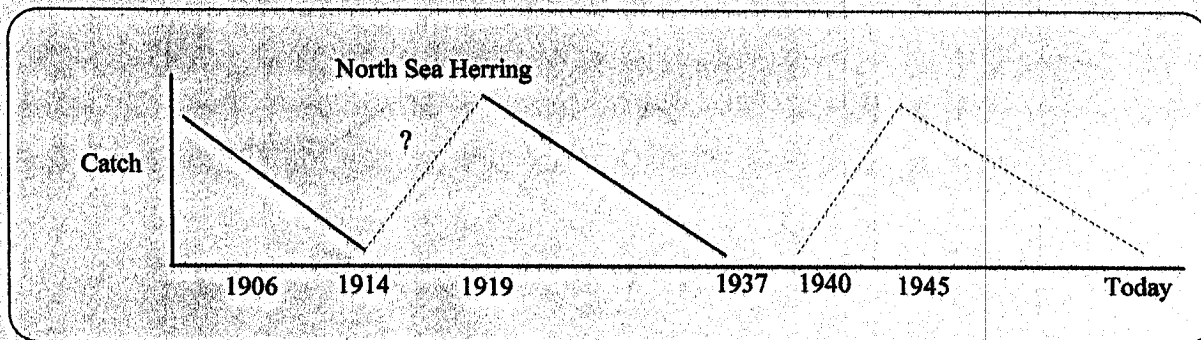
- Fraser River, BC, salmon recruitment cycle
 - Every 4th year class was large
 - Related to predator-prey interactions, not weather
 - Predator populations increased in response to large salmon year classes (numerical response)
 - Successive year classes were cropped heavily until predator population crashed
 - Next year class of salmon was large, then repeat cycle
 - A flood wiped out a whole salmon year class and reset the cycle
- Cycles easily noticed when regular
 - Recent advances in nonlinear dynamics (chaos theory) suggest looking for irregular recruitment cycles in "random" fluctuations

- ♦ Trends distinguishable from cycles by constant slopes and reversibility

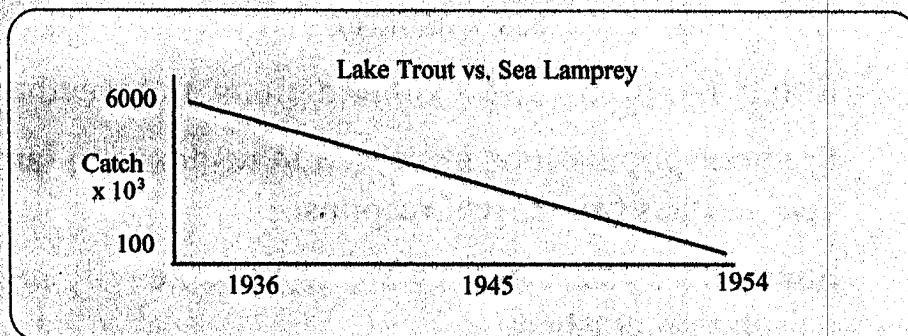
- Overfishing produces trends

E.g., N. Sea herring (WW I); Atlantic demersal fisheries (WW II)

Because there was no exploitation during the wars, stocks recovered only to be overfished again



- Lake trout/lamprey example in GL - combined with overfishing and pollution

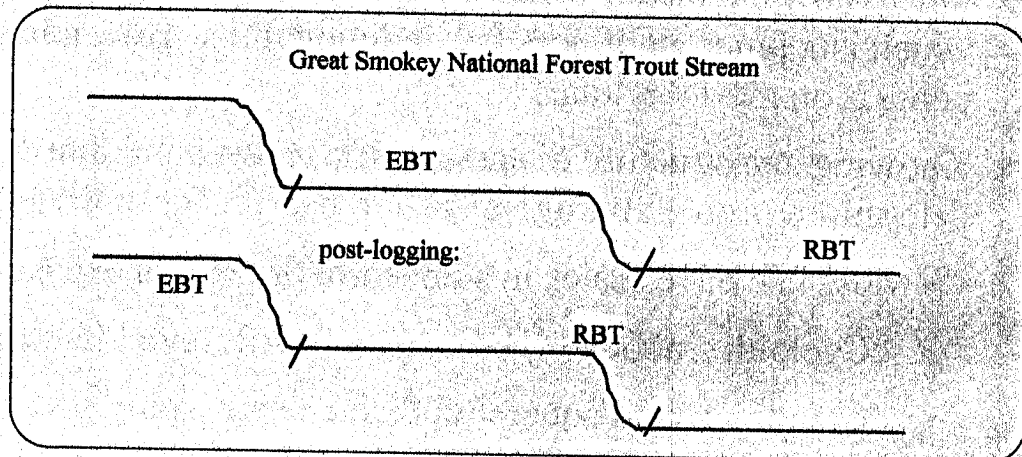


- Changed environmental conditions can also create trends in the sense of changing fishery population distributions

E.g., logging in Smokey Mts. shifted brook and rainbow trout upstream due to higher stream temperature/ turbidity

Because rainbows are superior competitors for territory, brook trout forced into coldest water/high gradient refuges

After national park/forest established, fish moved back downstream and brook trout reestablished dominance in high gradient reaches



Are trends reversible?

- ♦ If populations become too large, natural limiting factors regulate numbers
- ♦ If the causes of population decline are rectified and enough survivors are left to regenerate the population, a new trend of increase will appear
 - YOY survival will determine recruitment rates/recovery times
- ♦ If fishing pressure is too great for too long, populations may become so small that males and females don't meet or find the right habitats or extrapensatory mortality events may drive the population to extinction = recruitment overfishing
 - E.g., lake herring in L. Erie never recovered from overfishing in 1920s
 - E.g., lake trout vs. overfishing, lampreys
 - E.g., blue pike

How is individual fish growth incorporated in fishery yield models?

- ♦ Must know the rate at which weight is added to the population which is a function of how fast individual fish grow and population mortality rates
- ♦ Knowing age structure & age-specific growth and mortality rates determines proper size/age of fish to harvest for optimum yield

➤ Most fish have scales in skin: form protective exoskeleton

Cycloid: smooth-edged/circular = soft rayed fishes

Ctenoid: round/square/toothed edges = spiny rayed fishes

- ♦ Bony ridge scale development

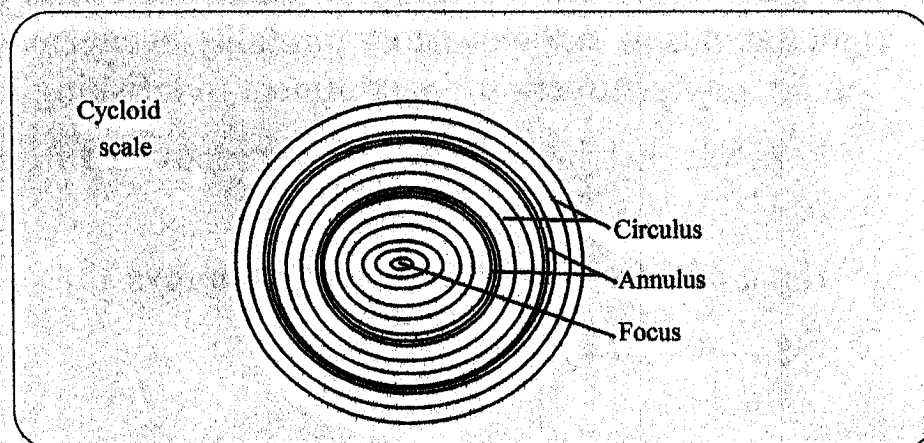
➤ Appear embryologically as tiny cell aggregates in caudal region that eventually spread over body

➤ Ridges of bone = circuli are laid around scale margins as fish grow, so scales grow as fish grows

➤ Circuli pattern changes annually in temperate fishes

Wider spacing during spring/summer feeding period;
narrower spacing in winter

Winter "mark" = annulus ---> ages/growth rates of fish

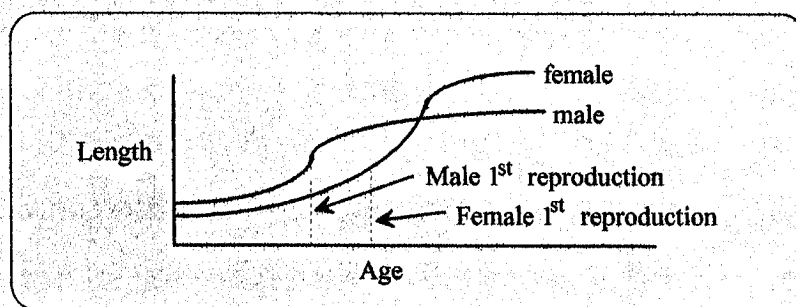


- ♦ For scale aging technique to be valid, 3 assumptions must hold
 - Scales are retained throughout life (true except for accidents)
 - Definite year marks are formed (true in temperate waters)

In climates with cold winters, growth usually stops and provides a clear annular mark (crowded, crossing circuli)
 - Scales and body size grow in definite ratio (can be figured)
- ♦ Each population has unique growth patterns, so scale aging method must be validated for each new population/location
- ♦ Scale length/body length relationships
 - If scales grow at the same rate as the body, then a simple isometric relationship holds: $S_a/S_t = L_a/L_t$ or $L_a = L_t * S_a/S_t$, where:
 - L_t = total fish length
 - L_a = fish length in past year 'a'
 - S_t = total scale length
 - S_a = distance to scale annulus formed in year 'a'
 - Not this simple, but empirical methods compensate
- ♦ What factors influence fish growth?
 - Temperature: grow more slowly in colder water (ectotherms)
 - Age: grow at ever decreasing rates as they age (devote more energy to producing gametes/maintaining larger body mass)
 - Population: 22 bluegill populations in Canadian lakes in Toronto area: range was $0.39 + 2.004 * S$ to $0.84 + 1.772 * S$
 - Sex: Often differences in males/females in same population

Sex differences in growth can be very important in setting safe size limits for harvesting a population

E.g., what would happen to the stock if the minimum harvest size was set at the size of male maturity or the average size at maturity?



Inflection points on curves indicate age/length at maturity = points where growth rates begin to slow

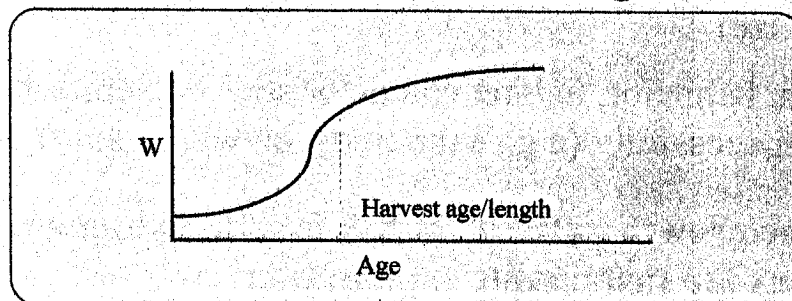
- ♦ Accurate scale length measures very important due to magnifying effect of multiplying $S_a/S_t * L_t$
 - Relatively small differences in actual/measured fish growth rates can produce $\pm 30\%$ differences in harvestable stocks predicted by models

Why all the fuss about fish growth relationships?

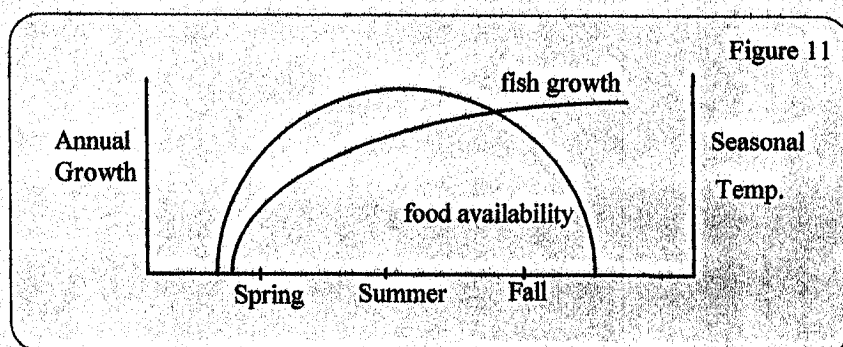
- ♦ A major goal of fishery studies is to develop a length-weight relationship to accurately predict the biomass of fish that can safely be harvested
 - Fishing gear tends to select fish more in relation to their length/girth than weight (net mesh size, surface area for electrofishing, etc.)
 - Also it is difficult to accurately weigh fish in the field (swaying scales) or after death (fluid loss)
 - A good length-weight relationship calculates accurate biomass of harvest by knowing only the lengths of the fish

Weight is highly correlated with length/age

- Growth in weight pattern indicates the age at which harvesting should take place = age at which growth rates peak



- ♦ Fish growth follows seasonal availability of food/temperatures
 - Earlier reproduction/hatching in spring ---> greater initial year's growth potential for YOY and greater survival chances for larger resulting juveniles (e.g., early vs. late bird clutches)
 - Growth rates decrease in mid-summer, because
 - Food availability peaks
 - High maintenance metabolism at high summer temperatures
 - With cooler fall temperatures, fish growth rates slow



- ♦ Growth rates can vary $\pm 30\%$ between years; Why?
 - Length of growing season
 - Temperature pattern: wide swings disrupt growth because each set of isozymes only works efficiently in a 2-5 C range
 - Population density: if fish compete for food, space, shelter, etc., the stresses involved can significantly reduce growth rates

- Predator to prey ratio (e.g., rapid growth of salmonids stocked into alewife filled LO followed by decrease in maximum salmon size)
- Location, behavior, habitat characteristics must match for fish to feed successfully (e.g., salmonids, alewives, smelt in LO)

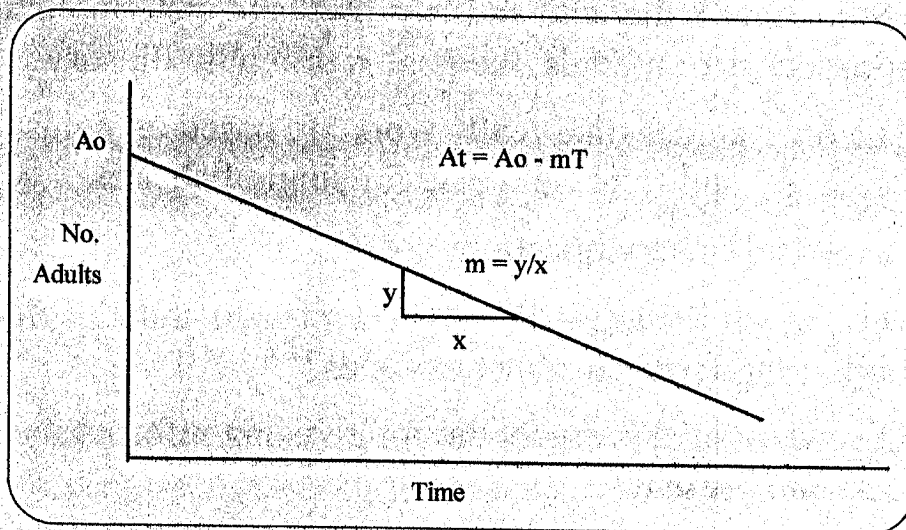
Understanding the growth patterns of fish is critical to managing fishery populations for sustainable exploitation

Purpose of fishery models is to assist understanding of fish population dynamics and make predictions: population size, growth, potential yield

- ♦ Useful theoretical fishery models have been sought since fishery populations began crashing in the North Sea around 1900
 - Given the complicated relationships that determine fish production in the wild and the simplistic, deterministic approaches of models, the goal is probably illusory
 - The only models that really work are based on painstakingly detailed, long-term field data for single fisheries
- ♦ The essential fishery questions are
 - How much fishing will a stock withstand and also maintain high, long-term, sustainable yields?
 - Can we predict = model the future using information from the past and present?
- ♦ All models have deficiencies, but these can be used to show us which factors require greater understanding
 - Theoretical models best used to help establish what important relationships are likely to be and to identify data gaps
- ♦ Models are mathematical equations or symbolic pictures that describe a dynamic ecological situation. They are used to
 - Relate in conceptual or quantitative ways various environmental and biological factors that influence fish populations/communities
 - Predict changes in a fishery based on changes in model parameters/assumptions
 - Provide predictions to enable informed setting of fishery regulations on quotas, size limits, gear restrictions, etc.

- ♦ E.g., A simple model to predict population size is $P = A + J$, where A = adult #, J = juvenile #, P = population size
 - The more information we have, the more complex the model can be and, theoretically, the more precisely it will predict population changes

E.g., If i = # adults migrating into a fishery stock and o = # juveniles migrating out, then $P = A + i + J - o$



- ♦ What other factors affect A and J ?; How could you model them?
 - E.g., mortality of adults: $A_t = A_0 - mT$, where A = number of adults at time t and time 0 (initial condition) and $-m$ = slope = mortality rate
- ♦ All variables in a fishery model are subject to many influences
 - E.g., " A " varies with productivity of water, availability of shelter, strengths of past year classes (which were strongly influenced by weather, predation, disease, fishing pressure, etc.)
 - Variables in models must be measurable/reasonably assumed

- ♦ To determine number/biomass of fish population, need to know
 - N = natural % mortality without exploitation
 - M = fishing % mortality
 - G = annual % growth
 - R = recruitment or number of catchable size fish entering population
- ♦ Russell (1931) was the first fishery biologist to formally recognize these relationships, and created conceptual model
 - "Russell Equation": $P_2 = P_1 + (R + G) - (N + M)$, where:
 - P_1, P_2 = resident stock sizes in years 1 and 2
 - R, G, N and M are additions or subtractions from the stock
 - In a correctly managed fishery, $P_2 = P_1$
 - How might each of these factors be modelled graphically?

No matter how complicated a fishery model may look, it always incorporates same factors found in Russell Equation (N, M, R, G)

- ♦ Equations describing these fundamental relationships over time can be complicated, non-linear, chaotic, etc.
- ♦ Traditional models use linear, deterministic equations that do not mimic real population dynamics well
 - New computer technology and math concepts (e.g., chaos theory) may improve the reliability of models
- ♦ Think of models as general descriptions of what the important relationships are in a system, not as accurate mimics of a system
 - Nature is too complicated to model completely

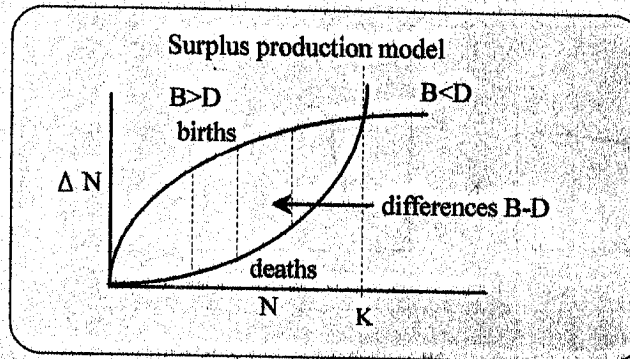
On an evolutionary scale, births and deaths must balance or waters would overflow with fish or populations would go extinct

- ♦ How can we fish at all without depleting stocks? Two escapes:
 - Fish generate far more fertilized eggs than can ever survive natural environmental conditions and limits. Corollaries:
 - Good environmental years permit higher than normal survival, and humans can harvest the surplus without reducing a stock below average carrying capacity
 - Sustainable yields and management concepts are fiction if we can only rely on weather, etc. to produce surplus yields
 - When stocks are thinned, their productivity increases by compensatory density dependent responses. Why?
 - Fewer individuals in a food filled, uncrowded environment will grow faster, increase reproductive output, and suffer lower mortality
 - For these natural ecological reasons, a well managed fish stock may exhibit faster growth, earlier 1st age of spawning, lower mortality, and greater juvenile survival than unfished stocks ---> sustainable, harvestable surplus

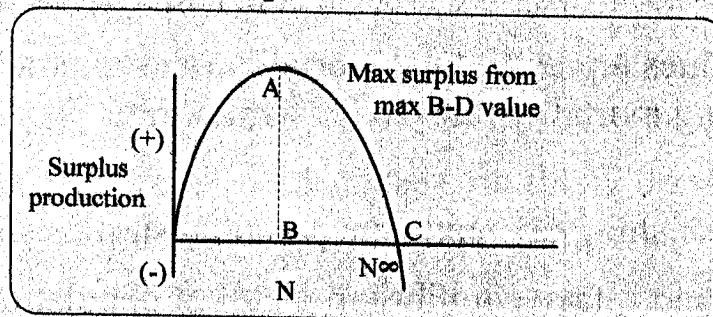
A surplus production model is a black box approach designed to take advantage of compensatory density dependent responses of fished populations

- ♦ SPMs consider only changing numbers/biomass of fish, not population dynamics of recruitment, growth and mortality
 - Surplus production = stock available for harvest without decreasing the generating stock size or capital
 - Stocks fluctuate due to density independent/dependent factors

- Density independent effects make relative birth/death relationships highly variable vs. smooth, theoretical graphs



- ♦ Relationship above is change in numbers vs. population size
 - Up to the carrying capacity, births exceed deaths
 - As K is approached, deaths accelerate/births decline - why?
- ♦ Greater distance between the birth/death curves ---> greater surplus production potentially available
 - The greatest distance between the birth and death curves is the population size that produces the maximum surplus

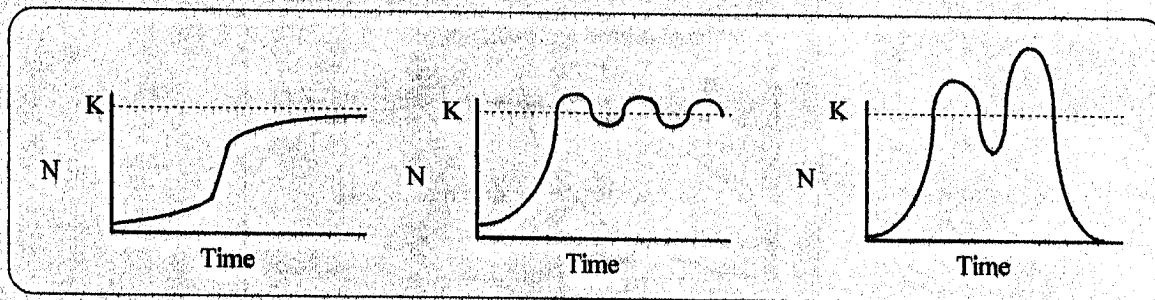


- ♦ The ratio of AB/BC above is a measure of stock resilience
 - The larger the AB/BC ratio becomes, the more unstable (less resilient) the population is in response to fishing

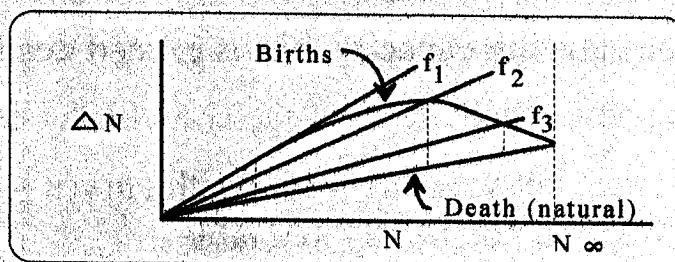
A large ratio means that the population size that produces the most offspring is very close to K

Therefore, any significant amount of fishing pressure rapidly depletes the population and may crash it

- Stock resilience ratios <1 , $1-2$, >2 ----> stable rise, stable oscillations around, unstable oscillations and crashes re: K



- ♦ There are as many sustainable yields as there are levels of fishing effort



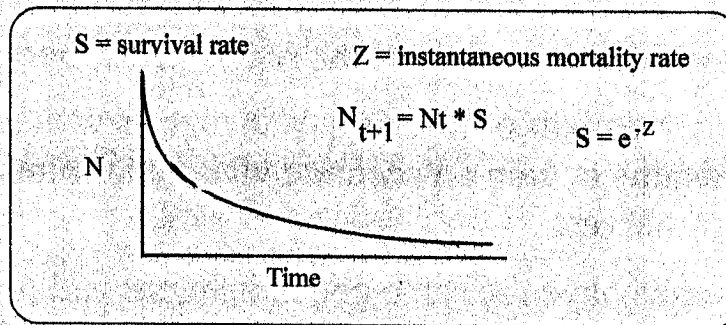
- Natural mortality plotted as linear function of increasing population size; otherwise a standard surplus production curve
- 'f' values represent total mortality rates after adding different fishing mortality rates to the natural rate
- While all yields are sustainable f_1 is overfishing/ f_3 is underfishing re: maximum potential surplus yields (MSY) = f_2
 f_1 and f_3 take equilibrium yields at population sizes smaller/larger than would produce maximum sustainable yield
 How might size and age structure in the fish population differ under f_1 and f_3 conditions?
 How might this affect population resilience to changing conditions?

Fishery models are based on weight more than numbers

- ♦ Must consider growth of individuals in size as well as numbers of births and deaths to gain an accurate view of surplus weight available for harvest
 - Such graphs have the same general shapes and properties as those for numbers only (see above)
- ♦ The rate of change of stock biomass (ΔB) depends on the weight of the stock and the difference between the stock biomass and the maximum equilibrium stock biomass (B_0)
 - On average, we can remove 1/4 of the carrying capacity biomass multiplied by the intrinsic rate of natural increase (r) each year
- ♦ SPMs consciously simplified to avoid having to determine difficult population dynamics data. Rests on assumptions
 - Changes in fishing effort are slow and regular
 - Equilibrium conditions only: rapid or great changes in fishing effort invalidate the model
 - Recruitment rates are stable or change slowly
 - No environmental trends affect overall stock production/biomass
- ♦ SPMs tend to work well for tuna, halibut and other fisheries that generally meet the assumptions

What about separate models for mortality, growth and recruitment when surplus production model assumptions are not met?

- ♦ Mortality: negative exponential depletion model assumes that constant proportion of a stock dies over each time interval and that no new individuals are added to a cohort



➤ $N_{t+1} = N_t * S$, where S = annual expectation of survival

➤ $Z = F + M$, where

Z = total instantaneous mortality rate

F = fishing mortality rate

M = natural mortality rate

➤ $S = e^{-Z} = e^{-(F+M)}$; therefore, $N_{t+1} = N_t * e^{-(F+M)}$

When $F = 0$, the function gives population depletion with natural mortality only

When F is very large, $N_{t+1} = 0$

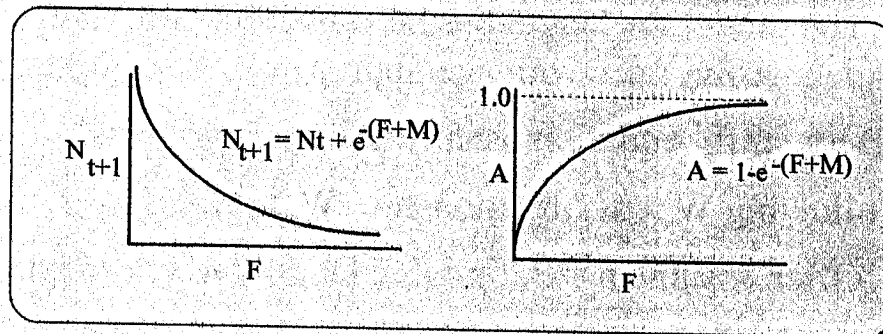
Therefore, model conforms to real world expectations

- ◆ These relationships allow us to model changes in fish stock size and total annual mortality in relation to fishing mortality

➤ A = annual expectation of total mortality = $1 - S$

Therefore, $A = 1 - e^{-(F+M)}$

➤ As F increases, population size decreases and annual mortality rises asymptotically to 1



- These relationships are used to determine F and M (M is hard to get directly for many fishes)
- As F gets large, $N \rightarrow 0 = C \rightarrow 100\%$ (1) because $F/(F+M)$ (from Baranov Catch Function) and $1 - e^{-(F+M)}$ both go to '1'

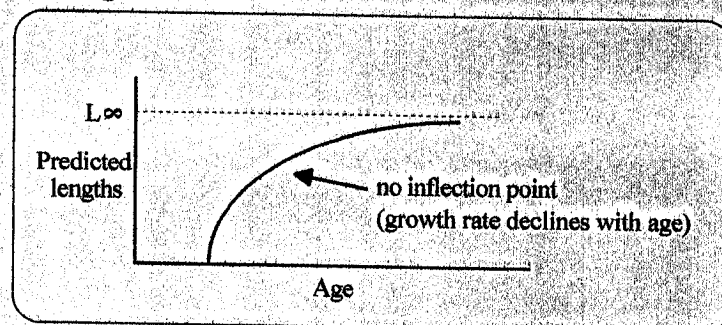
Growth models predict the rates at which individual fish add weight

- von Bertalanffy model is the most useful growth model for fishes

- Based on studies of growth in a variety of organisms: $dl/dt = c(L_0 - l_t)$,

where dl/dt = the rate of change of length, t = time, l = fish length, L_0 = maximum length attained by the species, a = growth constant from $W = aL^n$. Note: As $l_t \rightarrow L_0$, $dl/dt \rightarrow 0$

- The solution to the differential equation is: $l_t = L_0 * [1 - e^{-K(t-t_0)}]$, where t_0 = time when $l_t = 0$
- L_0 , K and t_0 can all be estimated from actual field growth data or they can be estimated by solving: $l_t = L_0 - (L_0 - l_0)e^{-kt}$ l_0 = initial length

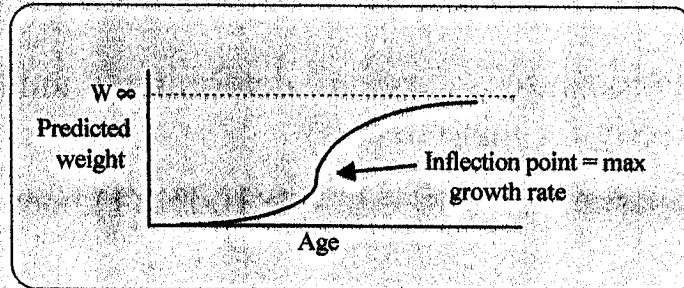


The model for length has no inflection point/fish grow at decreasing rates with age/approach L_0 asymptotically

- von Bertalanffy equation usually put on weight basis

➤ Following $W = aL^n$ relationship: $W_t = W_0 * [1 - e^{-K(t-t_0)}]^n$

Often assume $n = 3$, or cubic length-weight relationship

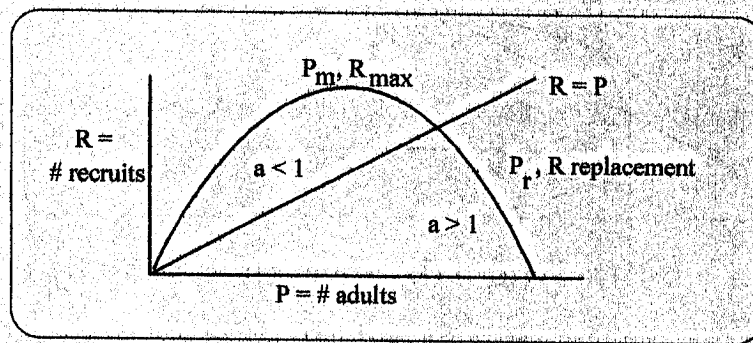


- Inflection point that indicates the age at which fish growth rates are maximum

The earlier or later harvests take place before or after this age the lower yields are likely to be (why?)

Recruitment models based on density dependent interactions even though density independent factors are generally more important

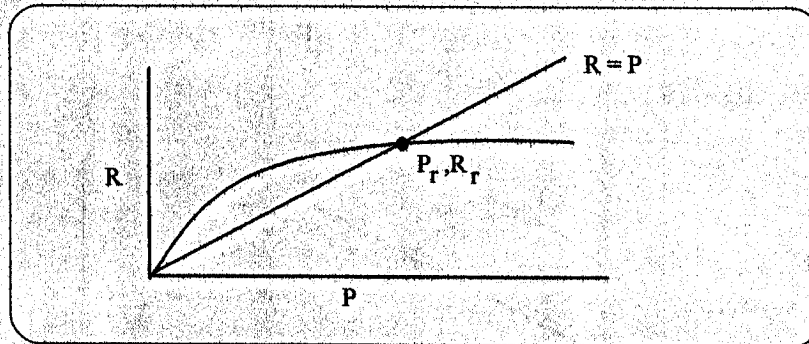
- ♦ Basic principle: as stock size approaches K , recruitment decreases
 - Ricker recruitment model: $R = aPe^{-bP}$, where R = # of recruits, P = # adults



- ♦ Important properties of model
 - Upper limit on recruitment regardless of stock size (peak)
 - Recruitment rate decreases past certain adult stock size; implies density dependent effects of adults on young
 - $R > P$ over some P values to compensate for mortality - otherwise the stock would always decline in numbers
 - Slope of curve (recruits per adult) is $dR/dP = ae^{-bP} * (1 - bP)$
- ♦ The key aspects of the model, all of which can be calculated when others are known from field data, are
 - R_m = maximum number of recruits = a/be
 - P_m = adult stock size that gives maximum recruitment = $1/b$
 - R_r = number of recruits needed just to replace adult stock = P_r
 - P_r = adult stock size that just replaces itself = $(\ln a)/b$
 - a = parameter for density independent effects on recruitment = e^{P_r/P_m}

➤ b = parameter for density dependent adult/recruit relations = $(\ln a)/P_r$

- ◆ Beverton and Holt also formulated a recruitment model



➤ $R = 1/(a + b/P) = P/(aP + b)$ after multiplying by P/P

Replacement value is found by setting $P = R$ and substituting: $(P_r = R_r) = R_r/(aR_r + b) = (1 - b)/a$

a & b derived from stock data, not calculated as by Ricker

- Differences from Ricker

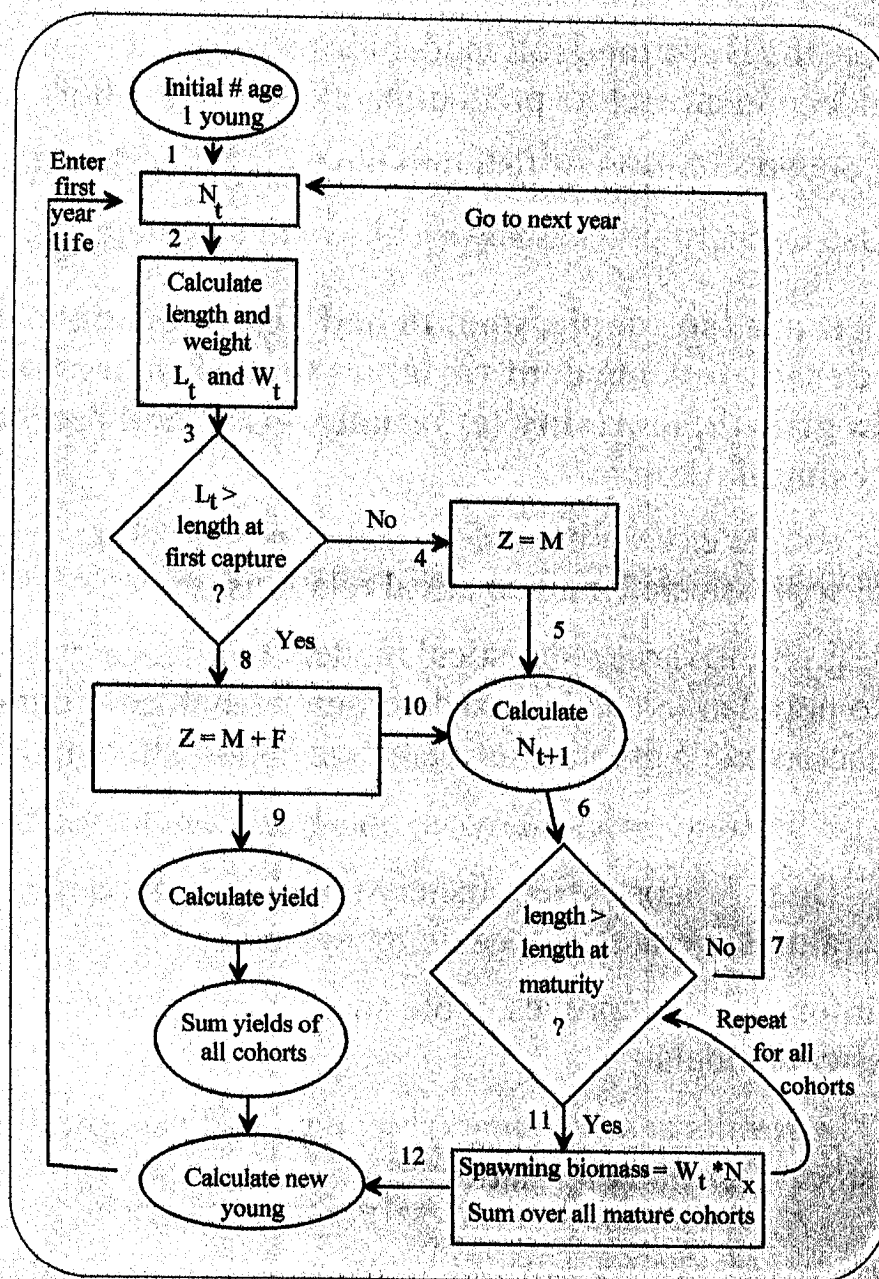
Recruitment does not decrease after passing R_m

$R_m = 1/a$ asymptote to recruitment axis (i.e., recruitment is controlled by density independent extrinsic environmental factors = true of most fish populations)

- Ricker worked with cod to make his model (density dependent and independent interactions influence recruitment)
- Beverton and Holt worked with herrings (density independent factors only influence recruitment)

Self-generating fishery stock models = putting it all together

- ◆ We have developed independent models for stock population dynamics: growth, mortality, recruitment
- ◆ How is it all put together to create a self-generating stock model that can incorporate data from a fishery to generate predictions about the future?

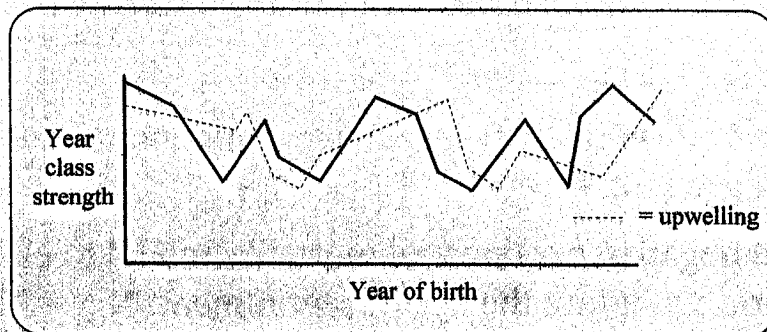


- Use von Bertalanffy size at age equation to model individual fish growth: $W_t = W_+ * [1 - e^{-k(t-t_0)}]^n$
- Use negative exponential mortality model to estimate natural mortality before the age of recruitment: $N_{t+1} = N_t * e^{-Mt}$
- Use the Baranov Catch Function to distinguish F and M after recruitment and to estimate catch: $C_t = N_t * (F/F+M) * (1 - e^{-(F+M)})$

- Use the Beverton-Holt model for recruitment (density independent factors predominate); $R = 1/(a + b/P)$
- Convert numbers of fish into biomass for each estimator
- Use iterative process shown above to calculate cohort yield

These models are too simple, smooth and deterministic to accurately mimic the density independent variables that cause most of the variation in growth, mortality (especially YOY) and recruitment in real fishery populations

- ♦ Must couple environmental variables to population dynamics with more sophisticated mathematical relationships
 - E.g., multivariate statistical models linking environmental data to population changes to determine which environmental factors have greatest influence on cohort strength/dynamics
 - E.g., time series analysis, non-linear or chaotic functions
 - Does "chaos" affect fishery population dynamics like it does atmospheric and oceanic processes?
- ♦ As information improves, more sophisticated models do replace classical models
 - The results can be remarkable; e.g., cod vs. upwelling stock-recruitment relationship

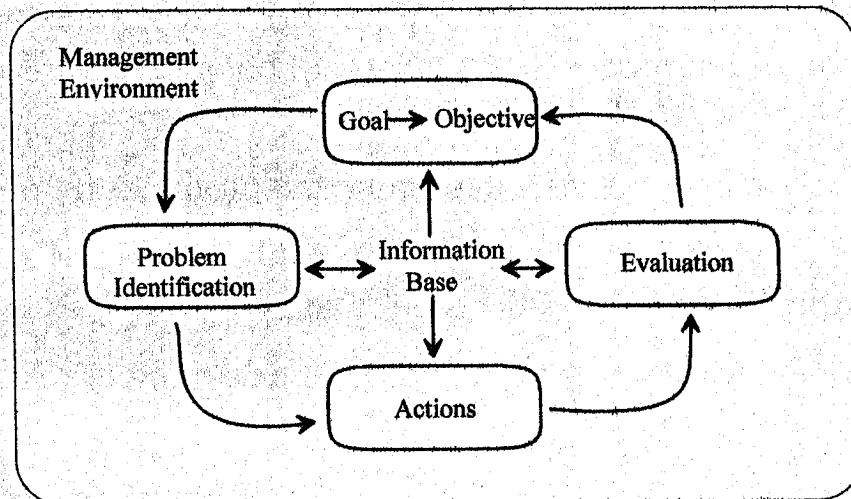


The importance of the classical models is to understand the development of fishery science and to appreciate how one goes about trying to generalize about and predict what will happen in a fishery

- ♦ Computers make sophisticated statistical modeling possible today
 - Despite the best computers, statistics and models, models rarely accurately predict what will happen in the future
 - Their value to guide for our thinking about what the important relationships are that determine the productivity of a fishery
- ♦ Experience and professional judgement are still the main ingredients of successful fishery management
 - No model is good enough to give us a number that will manage for us

Resource management is a cyclic process

- ♦ Set within an "environment" that has cultural, economic, political and ecological dimensions
- Information base supports five steps in management process



- Goal = statement of purpose about desired end result of a proposed management action or program

E.g., to develop a salmonid sport fishery in Lake Ontario

- Objective = specific, quantifiable step that will lead to fulfilling the management goal

E.g., stock 8 million salmonid fingerlings in the lake yearly

- Problem Identification: what prevents achieving an objective?

E.g., Lake Ontario tributaries can not support adequate salmonid reproduction

- Action = what is done to solve the problem/achieve objective

E.g., build the Altmar Hatchery that will provide 4 million chinook and 300,000 coho salmon annually for stocking

A more costly alternative not pursued was to restore natural forested watersheds around tributaries vis. 1800

➤ Evaluation = did management action achieve objective/goal?

Are we stocking 8 million healthy fish? (objective)

Is there a viable salmonid fishery? (goal)

- ♦ If evaluation reveals problems, repeat 5 step process until objectives and goal met

Despite complexities in the management environment, there are only five basic ways that fisheries can be managed

- ♦ Regulation of take
 - Regulates locations or seasons, gears or sizes, or quotas
 - Most fishery management uses this method
- ♦ Environmental maintenance and improvement
 - Improves the condition of aquatic habitat for fish and fishing by altering physical or chemical conditions
- ♦ Control of fish populations
 - Differential harvesting of species/age classes or control of undesirable members of an aquatic community
- ♦ Artificial propagation and distribution of fish to new waters
 - E.g., hatcheries and stocking
- ♦ Public education
 - Helps owners of resources understand principles of proper management in order to support it politically/economically

Regulation of take is the most important management method

- ♦ The basic methods include
 - Control the amount of fish taken (e.g., quotas or creel limits to spread catch among users, maintain minimum population size)

- Control the size of fish taken (e.g., mesh sizes, lake trout slot limit to protect sizes of first spawning)
- Control how fish are taken (gear restrictions; e.g., snagging, dynamite, fly fishing only)
 - Prevent destructive practices; e.g., turtle excluder devices (TEDs) and tuna/porpoise purse seining techniques
- Control when or where fish are taken (e.g., bass season opens after fry off nests; no fishing at night re: enforcement)
- Control who is allowed to take fish (e.g., limited entry)
- ♦ Good regulations designed to maintain harvests at optimum levels without being onerous, unenforceable or costly to the fishery
 - Use the minimum number needed to reach objectives
 - Most states have way too many
 - Regulations should make biological, economic, common sense
 - E.g., pros/cons for snagging salmon in LO tributaries
 - E.g., seasons vs. resorts - use creel limits, not shorter season
 - Goal is to provide maximum benefits (enjoyment, food, \$\$\$) for the maximum number of people
- ♦ Regulations must be enforceable and supported by a large majority of the public to be effective
 - E.g., 55 mph speed limits totally ignored = unenforceable
 - Must formulate regulations so that biological and economic interests are served optimally
 - Sacrificing the biological resource to 'save' the economy in the short-term leads to destruction of the resource and the economy long-term
 - E.g., Grand/Georges Bank and Pacific salmon fisheries

Habitat alteration/environmental control = 2nd management method

- ♦ Many land/water uses by humans alter potential for fisheries
 - Dam building and flood control projects alter river ecosystems and shoreline (most productive) habitat
 - Logging and human development severely damage watersheds that greatly impact aquatic ecosystems
- ♦ Types of remedial actions or control possible depend on location and type of water and type of fishery desired
 - Actions must be on an individual water body basis
- ♦ The three most important ways to preserve fish habitat and high fish production are
 - Maintain natural watersheds

In natural watersheds, habitats assume stable, natural characteristics of shade, cover, soil and water retention, temperature fluctuation, and fish production
 - Maintain natural seasonal water flows

Smoothing flood peaks and supplementing flows in the dry season protects fish and habitat

Flood control structures are much less expensive than trying to maintain constant flows
 - Control pollution; almost always cost effective
- ♦ Only manage habitat if damage is evident and other management remedies are more expensive

Population Control = 3rd major management method

- ♦ Justification is that population age-class structure or community species composition is not ideal for fishery production
 - Assumes we have fishery ecology data to know ideal situation

- ♦ Basic rationales for population control
 - Adjust age-class ratios (e.g., remove stunted adults to younger fish with higher growth potential grow; panfish, gamefish)
 - Adjust species ratios (e.g., reduce carp/bullheads re: turbidity/interference with game fish)
 - Control natural propagation (e.g., lamprey treatment with TFM in GL tributaries and bays; panfish nests to prevent stunting)
 - Change entire fishery (e.g., destroy non-brook trout populations in Adirondacks and stock with heritage strains)
- ♦ Many techniques used to control undesirable fish populations
 - Relax regulations that limit harvests; encourage anglers
 - Poisoning and restocking: destroy everything and start over
 - Seining and trapping (labor intensive; widely used to release desired sizes or species alive into the habitat)
 - Spawning site destruction (e.g., lower water levels at critical times to destroy year classes by exposing nests/nurseries)
- ♦ Draining a lake/stream and restocking
- ♦ Introducing predators
 - A huge success in the GL to control alewives
 - Can be a tricky ecological problem, especially when more than one prey species available
 - History of species introductions littered with disappointments (e.g., carp, alewives, lampreys, Asian catfish)

Artificial rearing and stocking = 4th major management method

- ♦ Ancient human practice
 - Carp and ornamental culture in Asia --> Europe in middle ages
 - N. American Indians spread pike, trout, bass, walleye, etc. throughout the Canadian shield lakes after glacial retreats
 - Fish culture began in U.S. in early 1800s (e.g., Caledonia Fish Hatchery founded by Seth Green in 1830s)
- ♦ Stocking is primary fishery management method re: money spent
 - Huge investments in hatchery facilities and personnel (e.g., Altmar near Pulaski cost \$14 million)
- ♦ Planting of fry was popular initially because of large numbers, short times in the hatchery, and low feeding costs
 - Has proved unworkable for several reasons

Mortality of planted fry follows same density independent mortality patterns as natural fry

The number of fry planted is usually insignificant vs. naturally produced numbers

E.g., Red Lakes, MN: 3.5 million female walleye -->
90K eggs each/year ---> fry to fingerling survival 5%
---> 3-8% survival to adulthood ---> 1.6 billion fry

Stocking max = 100 mil = 1/16th natural production!

Natural mortality of stocked fish always higher than natives

- Fry planting used for GL lake trout to try to stimulate attraction to potential spawning reefs

Three purposes for stocking: exotics, put & take, maintenance

- ♦ Introducing new or "exotic" species to a body of water
 - To restore or influence ecosystem conditions (e.g., salmonids in the GL, grass carp in weedy waters)
 - Species stocked for sentimental or food value (e.g., European colonists brought their favorite species with them: carp/trout)
 - Provide an exciting new fishery to a region (e.g., salmonids in GL, striped bass in southeast/midwest reservoirs)
- ♦ Put and take stocking designed to put hatchery product in creel as efficiently as possible
 - Water is temporary holding facility for catchable size fish
 - Best to stock fish of sizes minimally acceptable to anglers that can be raised in one year in a hatchery
 - Stocked fish are inferior competitors with natives and will die in a few weeks, so don't try to hide them from anglers!
 - Stocking rates determined by angling pressure and capacity of water body to hold fish
 - Stocking encourages more fishing and increases angling pressure (e.g., salmonid fishing in L. Ontario)
 - A variation on the put and take stocking method is put, grow and take (e.g., salmon stocking in oceans and Great Lakes)
- ♦ Maintenance stocking used in unusual circumstances where natural reproduction incapable of filling an otherwise suitable habitat with fish
 - E.g., lack of spawning habitat or suitable spawning environmental conditions
 - Technique used to keep fish populations close to carrying capacity (K) to provide optimum fishing opportunities

Public Education = 5th major management method

- ♦ For any management method to work well, managers must involve the fishing public in decision-making
 - Stakeholders must feel they have a meaningful say in how resources are used
- ♦ Presenting the public with pros and cons of alternative management actions gives agency a good sense of which alternatives are most acceptable
 - E.g., preference for 25-30" slot limit on lake trout in Lake Ontario vs. creel limit of one lake trout per day

Direct economic impact on eastern basin charter industry

Summary of fishery management ideas

- ♦ Five categories are regulation of take, environmental controls/habitat management, population controls, hatcheries/stocking, public education
- ♦ Properly conceived regulations generally provide the greatest fishery benefits for the least cost, but managers must carefully analyze each fishery to determine the best methods to employ
- ♦ The public strongly supports a better environment, but is very skeptical about government intelligence and waste

Base management decisions on solid research, common sense, public education/support